1996

Genetic gain for seed yield in soybean populations by recurrent selection

Michael Donald Uphoff
Iowa State University

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

Genetic gain for seed yield in soybean populations by recurrent selection

by

Michael Donald Uphoff

A dissertation submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Plant Breeding

Major Professor: Walter R. Fehr

Iowa State University

Ames, Iowa

1996

UMI
300 North Zeeb Road
Ann Arbor, MI 48103

Graduate College
Iowa State University

This is to certify that the Doctoral Dissertation of

Michael Donald Uphoff

has met the dissertation requirements of Iowa State University

Signature was redacted for privacy.

Major Professor

Signature was redacted for privacy.

For the Major Program

Signature was redacted for privacy.

For the Graduate College

TABLE OF CONTENTS

ABSTRACT	iv
INTRODUCTION	1
LITERATURE REVIEW	4
MATERIALS AND METHODS	13
RESULTS	19
DISCUSSION	29
CONCLUSION	31
APPENDIX	32
REFERENCES	57
ACKNOWLEDGMENTS	60

ABSTRACT

The purpose of the study was to compare genetic gain for seed yield associated with one and three generations of intermating between cycles of recurrent selection and the gain from evaluation of fewer lines from more single-cross populations or more lines from fewer single-cross populations. Three strategies of recurrent selection were conducted in the midseason maturity class and two strategies in the early and late maturity classes of the soybean population AP6. For the strategy designated 2ST-1IG, 100 F_4-derived lines from 45 single-cross populations were evaluated in each of three maturity classes, and the 10 highest yielding lines of each maturity class were intercrossed in a diallel to begin the next cycle. The strategy CB-2ST-1IG consisted of testing 100 F_4-derived lines from 10 single-cross populations in each of the three maturity classes and intermating 10 selected lines in a partial diallel to initiate the next cycle. For the strategy 2ST-3IG, 100 F_4-derived lines from an intermated population were tested in only the midseason maturity class, and the 10 highest yielding lines were intermated three generations to form the population for the next cycle. Composites of equal numbers of seeds of the parents for six cycles of 2ST-1IG and CB-2ST-1IG, four cycles of 2ST-3IG, and the individual parents of the most advanced cycles of each strategy were grown in replicated tests at three locations in Iowa during two yr. The genetic gain per cycle for seed yield was significantly greater with one generation of intermating between cycles (2ST-1IG and CB-2ST-1IG) than when three intermating generations were used (2ST-3IG). The genetic gain per cycle was greater for 2ST-1IG than for CB-2ST-1IG, although the differences were only significant for the early maturity class. The superior genetic gain for 2ST-1IG compared with the other methods indicated

that selection among progeny from the largest number of single-cross matings should maximize the yield improvement obtained from recurrent selection in soybeans.

INTRODUCTION

Recurrent selection has been used to improve quantitative traits in both cross- and self-pollinated crop species. All recurrent selection methods contain two fundamental steps: 1) Formation of a heterozygous and heterogeneous population through natural or artificial crossing and 2) identification of superior individuals to form a new population. The first recurrent selection strategy was published by Jenkins (1940). Hull (1945) was the first to use the term "recurrent selection" for population improvement. He later defined it as the process of selection over generations with crossing of selected plants to create genetic variability (Hull, 1952). To conduct a successful recurrent selection program, the following factors must be considered: 1) Specific breeding objectives, 2) a starting population with desirable characteristics, 3) a method of selection that will allow identification and incorporation of a large number of desirable alleles for quantitative traits, and 4) a population large enough to prevent fixation of undesirable alleles due to genetic drift (Comstock, 1977).

Recurrent selection in self-pollinated crops has been used successfully (Kenworthy and Brim, 1979; Prohaska and Fehr, 1981; Avey et al., 1982; Sumarno and Fehr, 1982). Several methods have been used to evaluate response to recurrent selection in soybean [Glycine max (L.) Merr.]. Miller and Fehr (1979) compared individual selected lines of cycle 0 and 1 populations to evaluate genetic gain for increased protein content. Kenworthy and Brim (1979), Brim and Burton (1979), and Sumarno and Fehr (1982) evaluated composites of selected lines from each cycle for evaluating genetic gain from selection for agronomic traits or protein content. They found that testing individual parents permits

comparison of the top selections from each cycle and determination of the cycle mean. A composite only provides information on the cycle mean. Composites can be used effectively for yield evaluation in soybeans if they are a representative sample of the entries for each cycle and if variability in maturity, height, or lodging is not excessive (Sumarno and Fehr, 1982).

Kenworthy and Brim (1979) and Sumarno and Fehr (1982) reported significant genetic gain for seed yield after three cycles of recurrent selection in which they evaluated lines for one year before selection of superior lines for crossing. Piper and Fehr (1987) and Guimaraes and Fehr (1989) reported that strategies that utilized one season of yield testing in hill plots were not as effective for identifying superior soybean genotypes as those that used two seasons of evaluation, including one season of row-plot tests.

The number of generations of intercrossing of parental lines is an important consideration for recurrent selection. A greater number of intermating generations should increase the chance of recombination, but will reduce the amount of genetic gain per year if the number of years per cycle is increased. Altman and Busch (1984) reported that no increases in the number of superior genotypes or genetic variances were found in three wheat populations after three generations of intercrossing. In soybean, recurrent selection with three generations of intermating was not superior to a conventional breeding strategy of one generation of intermating (Piper and Fehr, 1987; Guimaraes and Fehr, 1989).

The soybean population AP6 was formed to evaluate the effects of mating designs and methods of yield testing on recurrent selection for seed yield. The three methods used in AP6 were a conventional breeding strategy of one generation of intercrossing with a

limited number of single-crosses (CB-2ST-1IG), one generation of intercrossing by a diallel mating design without reciprocal crosses (2ST-1IG), and three generations of intercrossing between cycles (2ST-3IG). The objectives of this study were to compare the genetic gain from one and three intermatings between selection cycles and to determine if it is more beneficial to evaluate many lines from few populations or to test fewer lines from many populations.

LITERATURE REVIEW

Recurrent selection has been used to improve quantitatively inherited traits. Quantitative traits are controlled by many genes and are affected by the environment (Fehr, 1987). Under ideal circumstances, recurrent selection increases the frequency of favorable alleles in a population without a reduction in genetic variability (Hallauer, 1981).

Recurrent selection has been used in soybean and other self-pollinated crops to improve several traits. Kenworthy and Brim (1979) evaluated genetic gain for seed yield in soybean over three cycles of recurrent selection. The researchers used three criteria for selection: seed-yield per se; efficiency, measured as the ratio of total seed weight to total straw weight; and an index in which yield and efficiency were both weighted equally for selection. Through the evaluation of S_1-derived lines, they found that only yield per se was effective in increasing yield. The average rate of increase was 134 ± 30 kg ha^{-1} $cycle^{-1}$ for yield per se and 38 ± 55 kg ha^{-1} $cycle^{-1}$ for the index method. Yield decreased an average of 2 ± 47 kg ha^{-1} $cycle^{-1}$ by the efficiency method.

Sumarno and Fehr (1982) evaluated three cycles of recurrent selection for seed yield in the soybean population AP6. Forty high-yielding lines and cultivars of maturity groups 0 to IV were intermated for three generations to form the cycle 0 population. Cycle 0 lines were subdivided into early, midseason, and late maturity classes. A total of 100 F_4-derived lines from each maturity class were yield tested for one year at two locations with two replications of single-hill plots per location. The ten highest yielding parents per maturity class were selected and intermated the following season in a diallel without reciprocals. Cycle parent composites were evaluated to measure the response to

selection. An average yield increase of 120 ± 10 kg ha^{-1} $cycle^{-1}$ was found in the early maturity class and 24 ± 9 kg ha^{-1} $cycle^{-1}$ for the late class. No significant yield increase (-14 ± 8 kg ha^{-1} $cycle^{-1}$) was reported for the midseason class.

Piper and Fehr (1987) compared genetic gain among five different strategies of recurrent selection in the soybean population AP6. The strategies utilized one or three generations of intermating between cycles of selection and one or two stages of yield testing of F_4-derived lines to identify superior genotypes. The strategies included one stage of yield testing with one intermating generation, one stage of testing with three intermatings, a two-stage yield test with one intermating, and a two-stage yield test with three intermating generations. A fifth strategy was developed that reflected a conventional breeding design in which the progeny of a limited number of single-cross populations from one intermating generation were tested over two stages of yield testing. The response to selection was measured by evaluating parents of each cycle as composites. The average gain per cycle was 9.6 ± 1.1 g m^{-2} for the conventional breeding strategy, 6.0 ±1.1 g m^{-2} for the strategy with two stages of testing and one intermating, 5.5 ± 1.8 g m^{-2} for the two-stage test with three intermatings, 1.8 ± 0.6 g m^{-2} for the one-stage test and one intermating, and 0.3 ± 1.1 g m^{-2} for the one-stage test with three intermatings. The researchers concluded that yield gain was not increased by more than one generation of intermating per cycle and that identification of superior genotypes was enhanced by two stages of yield testing.

Recurrent selection for yield also has been used successfully in other self-pollinated species. Klein et al. (1993) evaluated three cycles of recurrent selection for test weight and

grain yield in oat (Avena sativa L.). The selection method involved intermating selected S_0-derived lines in the S_1 in a partial diallel to produce S_0 seeds. The S_0 plants were grown to produce S_0-derived lines. The lines were evaluated for test weight and seed-yield. Significant increases per cycle for average test weight occurred in populations selected for high test weight (17.8 ± 3.5 kg m^{-3}). Significant genetic gain per cycle for seed yield of 0.12 ± 0.07 Mg ha^{-1} was reported.

Stuthman and Stucker (1976) reported the results of testing two cycles of recurrent selection in an oat population. Cultivars chosen for superior seed yield were intermated for one generation in a diallel design. F_4-derived lines were obtained by single-seed descent and evaluated for yield. Superior lines were intermated in a partial diallel in the second cycle and $F_{4:6}$ lines were obtained for yield testing. In the cycle 2 population, yield increased an average of 33% compared with the cycle 0 parents.

Recurrent selection in cotton (Gossypium hirsutum L.) was used successfully to increase lint percentage (Meridith and Bridge, 1973). Plants were selected from the cotton cultivar 'Deltapine 523' for lint percentage and intermated by single crosses to form the cycle 1 population. Hybrid plants were advanced to the F_2 by selfing. Selection was initiated for lint percentage on an individual plant basis and then among progeny rows for two additional cycles of selection. Lint percentage increased an average of 4.2 compared with the cycle 0 population.

Miller and Fehr (1979) compared indirect and direct recurrent selection methods to increase seed protein content in soybean. High protein and high yielding lines were intermated three times to form the cycle 0 population. S_0-derived lines were evaluated for

seed composition and the 10 highest protein lines and the 10 lines with the lowest oil content were crossed in separate diallels to form two cycle 1 populations. Protein increased from 43.1 to 44.6% in the high protein population and from 43.1 to 43.9% in the low oil population after one cycle of selection. Direct selection was found to be a more effective method of increasing protein content than indirect selection for low oil.

Prohaska and Fehr (1981) used recurrent selection to increase iron-chlorosis resistance of a soybean population. The cycle 0 population was formed by intercrossing 10 cultivars or experimental lines and 10 plant introductions for three generations. All parents exhibited high levels of iron-chlorosis resistance. S_0-derived lines were tested on calcareous soil and the 10 most resistant lines were identified before flowering and crossed in a diallel. The researchers reported a 9% increase in resistance over the cycle 0 population after two cycles of selection.

Walker and Schmitthenner (1984) improved resistance to Phytophthora rot in soybean by recurrent selection. The cycle 0 population was formed by two generations of intermating 10 high yielding cultivars and lines with tolerance to Phytophthora infection. S_0 plants were grown in a winter nursery to obtain S_0-derived lines. Tolerant lines were selected from greenhouse evaluation and tested for a second time in the field. Lines were selected from the field trial and intermated to form the next cycle. After three cycles of selection, they observed a 21% increase in tolerance in the greenhouse test and a 10% increase under field conditions.

Recurrent selection has been used to modify oil quality in soybean. Carver et al. (1986) conducted eight cycles of recurrent selection with male-sterility to increase oleic

acid content in soybean oil. Plant introductions selected for high oleic acid content were intermated and superior F_4 progeny were selected. They were crossed to a male-sterile (ms_1 ms_1) line and fertile, selfed progeny were selected as the cycle 0 population. The population was planted in isolation to allow for intermating between male-sterile and fertile plants. Three cycles of recurrent phenotypic selection for high oleic content was initiated. In cycles 4 through 7, within half-sib family selection was performed. In those cycles, the progeny from selected male-fertile plants were grown at a winter nursery and planted in progeny rows. The male-fertile plant within each row with the highest oleic acid content was selected for intercrossing the following generation. S_0-derived line evaluation was initiated in cycle 8. Sterile plants were harvested individually and the progeny grown at the winter nursery in progeny rows. A single fertile plant was harvested per row. S_1 progeny were tested in single-row plots at two locations and two replications per location. Lines with the highest average oleic acid contents were selected. Oleic acid percentage increased by an average of 1.15 $\pm$ 0.17% per cycle under recurrent phenotypic selection, and by 2.64 $\pm$ 0.24% per cycle under half-sib family selection.

Other quantitative traits that have been improved by recurrent selection in soybean include seed size (Tinius et al., 1992) and photoperiod (Hanson, 1992).

Breeding programs for self-pollinated species most often utilize single-crosses between homozygous genotypes to generate new material for selection. Intermating in self-pollinated crops is costly and time consuming. Most breeding programs only include one generation of intermating between cycles of recurrent selection. Multiple generations of intercrossing between parents would increase the chance of recombination, may

increase the frequency of superior genotypes, would increase the number of seasons needed to complete a cycle, and may reduce genetic gain per year.

Hanson (1959) derived the average parental segment length per chromosome for multiple generations of intermating before selfing. He recommended that at least one or more and optimally four generations of intermating should be done before selfing to break up linkage groups and to increase recombinations within groups.

Bos (1977) performed a computer simulation to compare genotypic frequency of superior lines when F_2 plants were either selfed or intermated. The researcher specified a two-locus model in repulsion with the frequency of recombination ranging from 0.0039 to 0.5. For independent loci, no differences were found between selfed and intermated lines. With linked loci, the F_3 generation in the population where the F_2-derived lines were selfed had a higher frequency of superior homozygous lines than the intermated population. If selection was performed in the F_2, the intermated population had a 25% decrease in favorable homozygotes compared with the selfed population. This proportion decreased as the genes became more tightly linked.

Pederson (1974), in another computer simulation study, compared populations of homozygous lines intermated for 0, 1, or 2 generations in the F_2 with populations derived from selfing selected $F_{2:3}$ lines. Eight loci in eight different gene arrangements were included in the study. Loci were located on one, two, or three chromosomes. It was reported that both selection and intermating were equally effective in generating superior homozygous lines in five out of the eight gene arrangements. In the remaining combinations, intermating reduced the instance of superior homozygous lines.

Pederson (1974) also calculated the genetic variance for populations that were derived from 0, 1, or 2 generations of intermating in the F_2 generation. The author stated that if linked genes that control a single trait are in the repulsion phase, intermating will break them up and increase the frequency of desirable homozygotes. If genes are in the coupling phase, intermating would not be desirable. If coupling and repulsion phases are equally likely, intermating also could lead to the disruption of favorable gene complexes. Intermating would always increase genetic variance in instances when genes are located on short chromosome segments. When genes are located on longer chromosome segments, intermating, on average, also would be beneficial. There would also be instances when intermating would decrease genetic variance. Intermating when loci for a single trait are located on three or more long chromosome segments would not be beneficial.

Contradictory results have been observed in field experiments designed to determine the value of multiple generations of intermating before selection. Miller and Rawlings (1967) evaluated seven traits of F_2-derived lines in a cotton population that had been maintained in an isolation block for six generations beginning with the F_2. The natural mating system was a mixture of approximately 50% self pollination and 50% outcrossing. Random F_2-derived lines from the original population also were evaluated. The authors reported that intermating caused the genotypic variance to decrease for six traits in which coupling-phase linkage was expected. Fiber strength, a trait in which repulsion-phase linkage was suspected, had an increase in genotypic variance. These findings conformed with expectations that intermating tends to break up linkage blocks and reduce linkage disequilibrium.

Yunus and Paroda (1982) measured changes in correlation coefficients among traits in wheat (Triticum aestivum L.) when $F_{2:3}$ lines from single-cross matings were compared with $F_{2:3}$ lines derived by intercrossing random F_2 plants. They reported that intermating F_2 plants altered the correlations among traits in two crosses.

Altman and Busch (1984) studied three populations of spring wheat formed by three generations of random intermating. Crossing was facilitated by a male-sterility system controlled by a single dominant gene (S). Lines used as females in each population were heterozygous male-sterile (Ss) and male lines were homozygous recessive fertile (ss). Parents were selected for high-yield potential and grain protein percentage. Male fertile F_1 individuals were selfed to produce F_2-derived lines (I_0 lines) and 10 fertile and 10 sterile plants were randomly intercrossed to form the I_1 population. The I_2-I_4 populations were formed in a similar manner as I_1. For every cycle and population, the researchers tested 30 random F_2-derived lines and a composite of 75 F_2-derived lines. No increase in grain yield was found, except for I_3 in population 2. Plant height and lodging decreased in all populations for I_3 and I_4. The highest yielding lines of the I_3 and I_4 cycles of the three populations were similar to the highest yielding lines derived from the single crosses. Genetic variance estimates across cycles were highly erratic, and only two out of eighteen traits showed increases or decreases in genetic variance across cycles. Changes in correlation between grain yield and protein percentage, significance of which may be evidence for genetic recombination as a result of intermating, seemed to fluctuate in each population. The negative correlation was reduced in population 1, but was increased in population 3. The changes in correlation did not seem to have a genetic cause, but were

random in nature. The authors concluded that random intermating was not an effective means to enhance genetic recombination.

MATERIALS AND METHODS

AP6 was developed by intercrossing 40 high-yielding cultivars and experimental lines of maturity groups 0 to IV (Fehr and Ortiz, 1975). The population was used to compare alternative strategies of breeding with recurrent selection. The strategy designated CB-2ST-1IG was designed to represent selection in a manner similar to that of a conventional breeding (CB) program. A conventional breeding strategy generally involves evaluation of a relatively large number of individuals from each single-cross population. In contrast, recurrent selection programs commonly evaluate relatively few individuals from each single-cross mating. To form the cycle 0 population of this strategy, the 40 parents of AP6 were mated in a partial diallel of 30 single-crosses. Ten F4-derived lines inbred by single-seed descent from each of the 30 crosses were yield tested at two Iowa locations in hill plots. The three highest-yielding lines of each cross were evaluated for a second year (2ST) in row plots at three Iowa locations. For the test, the 90 lines were divided into early, midseason, and late maturity classes of 30 lines each. After the test, the 10 highest-yielding lines from each maturity class were selected as the parents of Cycle 1. An attempt was made to include as many of the original 40 parents as possible in the parentage of the lines selected for crossing. Each parent was crossed to another parent within the maturity class and to one of a different maturity class to obtain 30 single-cross populations with one intermating generation (IG).

To initiate the strategies designated 2ST-1IG and 2ST-3IG, the 40 parents of AP6 were intermated for three generations, as described by Fehr and Ortiz (1975). The populations were advanced to the $F_5(S_3)$ by single-seed descent to form the cycle 0 (C0)

population. A total of 300 F_5-derived lines from the C0 population were evaluated in the same manner as CB-2ST-1IG for 1 yr. The 30 highest yielding lines of each of the three maturity classes from the first-yield test were selected and tested for a second year in the same manner as CB-2ST-1IG. The 10 highest yielding lines of each maturity class from the second-year test were selected as parents of the C1 population. Therefore, the 30 lines selected from the C0 population are the common C1 parents of 2ST-1IG and 2ST-3IG. To form the cycle 1 population of the 2ST-1IG strategy, the 30 parents were intermated in a diallel without reciprocals and selfs to obtain 262 single-cross populations out of 435 matings that were attempted. Each of the single-cross populations was inbred by single-seed descent to obtain F_4-derived lines for evaluation.

For the 2ST-3IG strategy, the F_1 plants from the diallel of the 30 parents for 2ST-1IG were intermated (second intermating), and the F_1 plants from the second intermating were crossed for a third generation (3IG). The resulting population was inbred by single-seed descent to obtain F_4-derived lines of the C1 population for evaluation.

The second cycle of selection for all methods was conducted in the same manner as for the initial cycle, except for two changes. One change was that visual selection was performed during the first season of yield evaluation. Six-hundred F_4-derived lines were planted in replicated hill plots, and the two lines that originated from the same F_2 family were planted in adjacent plots in each replication. Only one of the two lines was harvested based on visual selection for uniformity of maturity and other desirable agronomic traits. The second change was that selected lines were crossed only to other lines within the same maturity class to form early, midseason, and late subpopulations for each strategy. For

CB-2ST-1IG, the 10 selected parents of a maturity class were mated in a partial diallel to form 10 single-cross populations, from which 200 F_4-derived lines were obtained for the first yield test. For 2ST-1IG, the 10 parents were mated in a diallel without reciprocals and selfs to form 45 single-cross populations from which 200 F_4-derived lines were obtained. For 2ST-3IG, the 10 parents were intermated for three generations before inbreeding was initiated to obtain 200 F_4-derived lines for testing.

Two seasons each year were used for crossing and generation advance at the Iowa State University nursery at the Isabela Substation of the University of Puerto Rico. One season in Iowa was used for crossing, generation advance, and replicated yield evaluation. CB-2ST-1IG and 2ST-1IG required 3 yr per cycle and 2ST-3IG required 4 yr per cycle of selection.

After two cycles of selection for 2ST-3IG, the genetic gain in the population was compared with 2ST-1IG and CB-2ST-1IG by Piper and Fehr (1987) and Guimares and Fehr (1989). The genetic gain in 2ST-3IG was not superior to the other strategies; therefore, continued selection in 2ST-3IG was limited to the midseason maturity class. By 1993, six cycles of CB-2ST-1IG and 2ST-1IG and four cycles of 2ST-3IG had been completed. In 1993 and 1994, the genetic gain was evaluated for all cycles. Sumarno and Fehr (1982) demonstrated that composites can be used effectively to evaluate genetic gain, if they are representative seed samples of the genotypes for each cycle. To make the composites for each cycle, strategy, and maturity class, an equal number of seeds of each parent was bulked to form the composite. There were 33 entries per experiment in the early and late maturity classes. These included one composite of the 13 early and 14 late

maturing parents of the C0, 12 composites of the 10 parents of each of six cycles for CB-2ST-1IG and 2ST-1IG, and the 10 individual parents of C6 for the two strategies. There were 66 entries in the experiment for the midseason class, including one composite of 13 midseason parents of the C0, 12 composites of the 10 parents of each of six cycles for CB-2ST-1IG and 2ST-1IG, three composites for the parents of C2 to C4 of 2ST-3IG, the 10 individual parents of C4 for each of the three strategies, and the 10 individual parents of C6 for CB-2ST-1IG and 2ST-1IG.

The experiments for each maturity class were evaluated at three locations in a randomized-complete block design with three replications per location. In 1993, the early maturity experiment was evaluated at Ames, Pomeroy, and Kanawha, the midseason experiment at Ames, Keystone, and Stuart, and the late maturity experiment at Ames, Fairfield, and Stuart. All locations in 1994 were the same as those in 1993, except that Pocahontas was used instead of Pomeroy for the early maturity experiment. The soil types at the sites were a Nicollet loam (fine-loamy, mixed, mesic, Aquic Hapludoll) at Ames, Kanawha, Pomeroy, Pocahontas and Fairfield, a Tama silty clay loam (fine-silty, mixed, mesic, Typic Argiudoll) at Keystone, and a Sharpsburg silty clay loam (fine montmorillontic, mesic, Typic Argiudoll) at Stuart. The plots consisted of four rows 4.6 m in length with 68 cm between rows. The planting rate was 33 seeds m^{-1} of row. To avoid competition effects between plots, only the middle two rows were harvested for yield. To avoid alley effects, the center rows were trimmed at maturity to 3.1 m with a hand sickle.

Maturity was recorded for each plot at two locations as the days after 31 August

when 95% of the pods had reached their mature color. Plant height was recorded on each plot at all locations as the average distance between the soil surface and the uppermost node on the main stem. Lodging was scored at maturity on a scale of 1.0 (all plants erect) to 5.0 (all plants prostrate) for all plots. Harvested seed was dried for approximately 72 hr at 40°C to achieve uniform moisture content before weighing.

Standard analyses of variance for the data combined over all locations were conducted on parental composites. The analysis was performed by the analysis of variance procedure (ANOVA) of the SAS software package (release 6.04) (SAS Institute, 1992). The model for the combined analysis of variance was as follows:

$$Y_{ijk} = \mu + E_i + R_{ij} + C_k + (EK)_{ij} + e_{ijk}$$

where Y_{ijk} = the observed value of the k^{th} composite of the j^{th} replicate at the i^{th} environment,

μ = the overall mean effect,

E_i = the effect of the i^{th} environment, I = 1 to 6,

R_{ij} = the effect of the j^{th} replicate in the i^{th} environment, j = 1 to 3,

C_k = the effect of the k^{th} composite, k = 1 to 13 (early and late maturity classes), k = 1 to 16 (midseason maturity class),

$(EC)_{ik}$ = the effect of the interaction between the i^{th} environment and the k^{th} composite, and

e_{ijk} = the error effect associated with the ijk^{th} observation.

The analysis of variance format is shown in Table 1. The composites and lines were considered fixed effects and environment was considered a random effect. The

Table 1. Form of the combined analysis of variance and mean squares.

Sources of Variation	Df	Mean Squares	Expected Mean Squares
Environments (E)	e-1		$\sigma^2 + c\sigma^2_{R/E} + rc\,\sigma^2_E$
Replications / E	e(r-1)		$\sigma^2 + c\sigma^2_{R/E}$
Composites (C)	c-1	M_1	$\sigma^2 + r\sigma^2_{CE} + reK^2_C$
C x E	(c-1)(r-1)	M_2	$\sigma^2 + r\sigma^2_{CE}$
Error	(r-1)[e(c-1)]	M_3	σ^2
Total	erc-1		

composite X environment interaction mean squares were used to test the significance of the main effect of composites. The significance of the composite X environment mean squares was tested with the error mean square. Response to selection was determined with respect to the composite of cycle 0 parents included in each maturity class. A regression of cycle mean on cycle number was calculated to estimate genetic gain per cycle by means of the general linear models procedure (GLM) of SAS (SAS Institute, 1992). Standard errors of the regression coefficients were calculated by a method similar to that described by Steel and Torrie (1980).

RESULTS

Significant differences in yield were found among composites in all maturity classes (Tables 2 and 3). The composite X environment interaction was significant in the midseason maturity class, but was not significant in the early and late maturity classes.

In the early maturity class, there was a significant yield increase from the C0 to the C6 of 511 kg ha^{-1} for 2ST-1IG and of 233 kg ha^{-1} for CB-2ST-1IG. The linear regression coefficients of cycle mean yield on cycle number were significantly different from zero for 2ST-1IG and CB-2ST-1IG (Table 4). The genetic gain per cycle for 2ST-1IG was significantly greater than that of CB-2ST-1IG ($P < 0.01$) (Table 4). The highest-yielding parent of C6 for 2ST-1IG was superior to the highest yielding parent of CB-2ST-1IG (Table 5).

In the midseason class, significant yield differences were found between the C0 and C4 composites of 2ST-1IG (215 kg ha^{-1}) and of CB-2ST-1IG (366 kg ha^{-1}) (Table 3). The yield difference between C0 and C4 of 43 kg ha^{-1} for 2ST-3IG was not significant. Significant differences in yield were found between the C0 and C6 of 2ST-1IG (282 kg ha^{-1}) and of CB-2ST-1IG (386 kg ha^{-1}). The linear regression coefficients for cycle mean yield on cycle number were significant for 2ST-1IG and CB-2ST-1IG, but not for 2ST-3IG (Table 4). The genetic gain for 2ST-1IG was significantly greater than that of 2ST-3IG, but not significantly greater than that of CB-2ST-1IG. The highest yielding parent in C4 for each strategy was similar in performance. CB-2ST-1IG had higher yielding parents in C6 than the parents of 2ST-1IG.

For the late maturity class, the differences in yield between the C0 and C6

Table 2. Combined analysis of variance for yield over six environments for the early, midseason, and late sets.

		Mean squares[b]		
Sources of variation	Df	Early	Midseason	Late
Environments (E)	5	1588.0**	367.2**	1751.5**
Replications / E	12	45.0**	1.9**	17.5**
Composites (C)	12 (15)[a]	49.8**	5.3**	43.2**
C x E	60(75)	4.7	1.1**	4.5
Error	144(180)	4.1	0.7	5.1

[a]Values in parentheses are the degrees of freedom associated with the sources of variation for the midseason set.

[b]Mean squares should be multiplied by 10^4 to obtain the actual value.

**Significant at the 0.05 and 0.01 probability levels, respectively.

composites of 2ST-1IG (312 kg ha^{-1}) and of CB-2ST-1IG (421 kg ha^{-1}) were significant. The linear regression coefficients were significantly different from zero for 2ST-1IG and CB-2ST-1IG (Table 4). The genetic gains for 2ST-1IG and CB-2ST-1IG were not significantly different. The highest yielding parent in C6 for CB-2ST-1IG was superior to the highest yielding parent of 2ST-1IG (Table 5).

There were significant differences in maturity among composites and the composite X environment interaction was significant in all maturity classes (Table 6). In the early maturity experiment, some of the parents used to form the C0 were outside the maturity range used to select parents for subsequent cycles of the early maturity class. Consequently, there was a significant difference in maturity between the C0 and the

Table 3. Mean yields of parental composites for three strategies of recurrent selection averaged over six environments.

Method	Cycle	Early	Midseason	Late
		----------	kg ha^{-1}	----------
	0	2733	2689	2916
2ST-1IG	1	2791	2694	2947
	2	2838	2736	2975
	3	2921	2894	3094
	4	3169	2904	3093
	5	3160	2940	3068
	6	3244	2971	3230
CB-2ST-1IG	1	2721	2765	2948
	2	2916	2794	3165
	3	2915	2910	3139
	4	3061	3055	3390
	5	2939	2925	3284
	6	2966	3075	3339
2ST-3IG	1		2694	
	2		2665	
	3		2808	
	4		2732	
$LSD_{0.05}$		135	135	148
SE		68	68	75

Table 4. Coefficients for the linear regression of cycle mean yield on cycle number.

Method	Early[a]	Midseason	Late
	---------- kg ha^{-1} ----------		
2ST-1IG	93.0** ± 9.0 a	53.8** ± 8.0 a	46.3** ± 10.8 a
CB-2ST-1IG	23.0* ± 9.8 b	31.0** ± 12.2 ac	38.7** ± 7.4 a
2ST-3IG		3.5 ± 15.7 bc	

[a]Within maturity classes, regression coefficients followed by the same letter were not significantly different at $P < 0.05$.

*,** Linear regression coefficients significantly different from zero at the 0.05 and 0.01 probability levels, respectively.

Table 5. Range of mean yields for individual parents of cycles 4 and 6 for the midseason class and cycle 6 for the early and late classes.

Method	Cycle	Early	Midseason	Late
		---------- kg ha^{-1} ----------		
2ST-1IG	4		2684-3040	
CB-2ST-1IG	4		2894-3069	
2ST-3IG	4		2490-3037	
2ST-1IG	6	3016-3392	2700-3037	3033-3129
CB-2ST-1IG	6	2837-3157	2880-3224	3016-3568

Table 6. Combined analysis of variance for maturity over six environments for the early, midseason, and late maturity classes.

		Mean squares		
Sources of variation	Df	Early	Midseason	Late
Environments (E)	5	2377.1**	2241.3**	1021.0**
Replications / E	8	3.9	2.2	5.0
Composites (C)	12 (15)[a]	61.3**	25.1**	10.2**
C x E	36(45)	5.7**	8.3**	3.3*
Error	96(120)	2.1	3.0	1.9

[a]Values in parentheses are the degrees of freedom associated with the sources of variation for the midseason set.

**Significant at the 0.05 and 0.01 probability levels, respectively.

composites of the other cycles (Table 7). There were no consistent trends for changes in maturity between the C1 and C6 for any of the strategies in the three maturity classes. Linear regression coefficients for maturity were significant for 2ST-1IG and CB-2ST-1IG in the early maturity class (Table 8).

Significant variation was found among composites and the composite X environment interaction was significant for lodging score in the three maturity classes (Table 9). There were significant differences among composites for height (Table 10). The composite X environment interaction was significant for height in the midseason maturity class, but was not significant in the early and late maturity classes (Table 10). The mean lodging scores and plant height for 2ST-1IG and CB-2ST-1IG decreased across cycles of selection (Table 7). There was no consistent change in the mean lodging scores and plant height for

Table 7. Maturity, lodging and plant height of parental composites for three strategies of recurrent selection in one or three maturity classes averaged over six environments.

		Early			Midseason			Late		
Method	Cycle	Mat.[a]	Lodg.[b]	Ht.	Mat.	Lodg.	Ht.	Mat.	Lodg.	Ht.
		--days--	--score--	--cm--	--days--	--score--	--cm--	--days--	--score--	--cm--
Cycle 0		14	2.2	80	20	1.9	96	31	2.1	109
2ST-1IG	1	20	2.0	93	22	2.1	103	30	2.5	105
	2	21	1.9	91	23	2.3	103	28	2.3	102
	3	20	1.7	88	21	1.8	92	30	2.3	103
	4	18	1.8	83	21	1.8	95	30	2.1	107
	5	20	1.7	82	21	1.9	95	30	2.1	100
	6	22	1.8	85	21	1.8	91	30	2.2	98
CB-2ST-1IG	1	20	2.0	85	24	2.2	99	28	2.4	105
	2	22	1.8	86	23	2.4	95	28	2.2	99
	3	20	1.7	80	24	2.1	90	30	2.4	104

[a] Days after August 31 when 95% of the pods have reached the mature color.

[b] Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table 7. (continued)

Method	Cycle	Early			Midseason			Late		
		Mat.[a]	Lodg.[b]	Ht.	Mat.	Lodg.	Ht.	Mat.	Lodg.	Ht.
		--days--	--score--	--cm--	--days--	--score--	--cm--	--days--	--score--	--cm--
CB-2ST-1IG	4	19	1.6	79	22	2.0	90	30	2.1	102
	5	23	1.6	83	23	2.0	91	30	2.4	99
	6	21	1.6	80	23	1.7	88	29	2.0	101
2ST-3IG	1				22	2.1	103			
	2				25	2.4	105			
	3				22	2.1	109			
	4				25	2.4	101			
$LSD_{0.05}$		1	0.3	5	1	0.2	4	1	0.2	5
SE		1	0.2	3	1	0.1	2	1	0.1	3

Table 8. Regression coefficients for maturity, lodging, and plant height per cycle for early, midseason, and late maturity classes averaged across six environments.

Maturity class	Method	Maturity	Lodging	Height
		----------days[a]----------	----------score[b]----------	----------cm----------
Early	2ST-1IG	0.79 ± 0.15**	-0.67 ± 0.31*	-0.55 ± 0.44*
	CB-2ST-1IG	0.91 ± 0.14**	-1.01 ± 0.34**	-0.32 ± 0.37
Midseason	2ST-1IG	-0.07 ± 0.09	-0.45 ± 0.23*	-1.33 ± 0.27**
	CB-2ST-1IG	0.30 ± 0.32	-0.42 ± 0.24*	-1.49 ± 0.27**
	2ST-3IG	0.95 ± 0.91	1.00 ± 0.94	-0.62 ± 0.57
Late	2ST-1IG	-0.04 ± 0.12	-0.34 ± 0.26*	-0.77 ± 0.28**
	CB-2ST-1IG	-0.03 ± 0.09	0.14 ± 0.25	-1.15 ± 0.38**

*,**Significantly different from zero at the 0.01 and 0.05 probability levels, respectively.

[a]Days after August 31 when 95% of the pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table 9. Combined analysis of variance for lodging over six environments for the early, midseason, and late maturity classes.

		Mean squares		
Sources of variation	Df	Early	Midseason	Late
Environments (E)	5	700.0**	1393.6**	1376.0**
Replications / E	12	32.4	21.0	63.0**
Composites (C)	12 (15)[a]	57.7**	91.1**	43.3**
C x E	60(75)	35.1**	31.1**	33.2**
Error	144(180)	23.0	12.5	13.6

[a]Values in parentheses are the degrees of freedom associated with the sources of variation for the midseason set.

**Significant at the 0.05 and 0.01 probability levels, respectively.

Table 10. Combined analysis of variance for height over six environments for the early, midseason, and late maturity classes.

		Mean squares		
Sources of variation	Df	Early	Midseason	Late
Environments (E)	5	11041.6**	13537.4**	12437.7**
Replications / E	12	246.9**	124.4**	68.9
Composites (C)	12 (15)[a]	344.1**	692.4**	178.3**
C x E	60(75)	65.1	57.9**	59.5
Error	144(180)	65.9	36.9	58.0

[a]Values in parentheses are the degrees of freedom associated with the sources of variation for the midseason set.

**Significant at the 0.05 and 0.01 probability levels, respectively.

2ST-3IG across selection cycles. The C4 parents of 2ST-3IG exhibited significantly greater lodging and plant height than the C4 parents of the other two strategies. The mean performance of the C6 parents for the two traits were not significantly different in any of the maturity classes for the two selection strategies. Linear regression coefficients for decreases in lodging score were significant for 2ST-1IG and CB-2ST-1IG in both the early and midseason maturity classes and for 2ST-1IG in the late maturity class (Table 8). Regression coefficients for decreases in height were significant for all methods, except for CB-2ST-1IG in the early maturity class and 2ST-3IG in the midseason maturity class (Table 8).

DISCUSSION

An objective of this study was to evaluate genetic gain for seed yield associated with one intermating generation versus three intermating generations between cycles of selection. Hanson (1959) indicated that multiple generations of intermating should be considered in soybeans to increase genetic recombination. One generation of intermating for 2ST-1IG and CB-2ST-1IG was superior in genetic gain per cycle to three intermating generations for 2ST-3IG. These results supported the earlier findings of Piper and Fehr (1987) and Guimaraes and Fehr (1989) who found no benefit from more than one generation of intermating after two cycles of selection in AP6. The advantage for one intermating is even greater if genetic gain was calculated per year instead of per cycle. With three seasons available per year, an extra year was required to perform three intermatings rather than one. This increased the cost of each cycle because of the labor and other resources needed to carry out three intermatings instead of one. The superiority of one generation of intermating agrees with Altman and Busch (1984) in wheat. They reported no increase in the number of superior genotypes or in the genetic variance estimates for three intermating generations compared with one intermating generation.

Another objective of the study was to evaluate the genetic gain associated with evaluation of fewer lines from more single-cross populations (2ST-1IG) compared with the gain associated with testing more lines from fewer single-cross populations (CB-2ST-1IG). The genetic gains per cycle for 2ST-1IG were greater than for CB-2ST-1IG in each maturity class, but the difference was only significant in the early maturity class. The results did not agree with those of Piper and Fehr (1987) and Guimaraes and Fehr (1989)

who reported that the average genetic gain per cycle in AP6 for CB-2ST-1IG (32 kg ha^{-1}) was greater than that of 2ST-1IG (14 kg ha^{-1}) after three cycles of selection. One potential advantage of evaluating fewer lines from more populations relates to the mean inbreeding of the population (Miller and Fehr, 1979). By evaluating two or three lines from 30 single crosses in 2ST-1IG, it was easier to select superior lines with different parentages than when 10 lines were evaluated from only 10 single-crosses in CB-2ST-1IG. The advantage may have become more important in more advanced cycles of selection.

Selection for seed yield did not have a negative influence on maturity, lodging, or plant height. Selection of parents within a narrow maturity range prevented changes in days to maturity across cycles of selection. Miller and Fehr (1979) also reported that selection of parents within a defined maturity range during recurrent selection for soybean seed protein was effective in preventing shifts in the mean maturity of a population.

CONCLUSION

Increasing the number of generations of intermating was not found to be an effective method of increasing genetic gain for seed yield. Genetic gain was greater for one generation of intermating between selection cycles than three generations of intermating. When designing a recurrent selection program for seed yield in soybeans, the researcher would maximize genetic gain by increasing the number of cycles of selection rather than the number of generations of intermating per cycle. The larger genetic gain for 2ST-1IG compared to CB-2ST-1IG indicated that selection among progeny from the largest number of single-cross matings possible maximizes the yield improvement obtained from recurrent selection.

Days to maturity, plant height, and lodging scores were not adversely affected by selection for seed yield.

APPENDIX

Table A1. Mean agronomic traits of parent composites for each strategy of the early maturity class grown at Ames, IA in 1993.

Entry		Yield	Maturity	Lodging	Height
		----kg ha^{-1}----	----days[a]----	----score[b]----	----cm----
	C0	2746	16	1.6	79
2ST-1IG	C1	2593	25	1.8	83
	C2	2501	27	1.7	87
	C3	2934	25	1.6	81
	C4	3145	25	1.5	79
	C5	2938	26	1.4	73
	C6	3102	27	1.7	78
CB-2ST-1IG	C1	2679	26	1.6	80
	C2	2930	26	1.7	77
	C3	2824	27	1.5	72
	C4	2824	25	1.5	71
	C5	2781	27	1.5	72
	C6	2954	27	1.4	79
$LSD_{0.05}$		263	2	0.2	13
SE		127	1	0.1	6

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A2. Mean agronomic traits of parent composites for each strategy of the early maturity class grown at Pomeroy, IA in 1993.

Entry		Yield	Lodging	Height
		----kg ha^{-1}----	----score[a]----	----cm----
	C0	2504	1.3	65
2ST-1IG	C1	2547	1.5	76
	C2	2640	1.3	74
	C3	2708	1.7	76
	C4	2832	1.4	74
	C5	2819	1.5	72
	C6	2851	1.3	72
CB-2ST-1IG	C1	2634	1.3	72
	C2	2597	1.3	75
	C3	2703	1.3	68
	C4	2793	1.3	71
	C5	2649	1.3	73
	C6	2656	1.3	63
$LSD_{0.05}$		319	0.2	9
SE		154	0.1	5

[a]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A3. Mean agronomic traits of parent composites for each strategy of the early maturity class grown at Kanawha, IA in 1993.

Entry		Yield	Maturity	Lodging	Height
		-----kg ha^{-1}-----	-----days[a]-----	-----score[b]-----	-----cm-----
	C0	1805	24	1.0	57
2ST-1IG	C1	2054	28	1.3	62
	C2	2115	26	1.3	65
	C3	1960	28	1.5	66
	C4	2110	26	1.3	55
	C5	2323	27	1.5	65
	C6	2484	32	1.5	67
CB-2ST-1IG	C1	1743	28	1.3	62
	C2	2157	30	1.1	59
	C3	1994	26	1.2	55
	C4	2071	26	1.4	54
	C5	1981	29	1.3	60
	C6	2022	31	1.3	60
$LSD_{0.05}$		347	3	0.3	12
SE		174	2	0.2	6

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A4. Mean agronomic traits of parent composites for each strategy of the midseason maturity class grown at Ames, IA in 1993.

Entry		Yield	Maturity	Lodging	Height
		-----kg ha^{-1}-----	-----days[a]-----	-----score[b]-----	-----cm-----
	C0	2537	28	1.7	87
2ST-1IG	C1	2451	30	2.1	86
	C2	2563	30	2.2	97
	C3	2755	28	2.1	81
	C4	2719	29	2.1	89
	C5	2921	29	2.4	91
	C6	2788	30	2.2	76
CB-2ST-1IG	C1	2619	30	2.0	84
	C2	2664	29	2.4	89
	C3	2873	29	2.1	88
	C4	2933	30	2.1	78
	C5	2834	31	2.1	84
	C6	3019	30	2.2	81
2ST-1IG	C2	2408	30	2.6	94
	C3	2657	29	2.1	95
	C4	2669	30	2.2	81
$LSD_{0.05}$		252	1	0.4	11
SE		127	1	0.1	6

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A5. Mean agronomic traits of parent composites for each strategy of the midseason maturity class grown at Stuart, IA in 1993.

Entry		Yield	Lodging	Height
		-----kg ha^{-1}-----	-----score[a]-----	-----cm-----
	C0	1709	1.1	67
2ST-1IG	C1	1936	1.2	71
	C2	1973	1.2	73
	C3	2007	1.1	65
	C4	2167	1.3	67
	C5	2018	1.1	66
	C6	2060	1.3	64
CB-2ST-1IG	C1	1713	1.5	72
	C2	1838	1.1	64
	C3	1731	1.1	59
	C4	1871	1.1	61
	C5	2048	1.2	67
	C6	2159	1.1	66
2ST-3IG	C2	1919	1.3	77
	C3	2065	1.4	78
	C4	2019	1.3	69
$LSD_{0.05}$		310	0.2	11
SE		155	0.1	5

[a]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A6. Mean agronomic traits of parent composites for each strategy of the midseason maturity class grown at Keystone, IA in 1993.

Entry		Yield	Maturity	Lodging	Height
		-----kg ha^{-1}-----	-----days[a]-----	-----score[b]-----	-----cm-----
	C0	2762	24	1.5	98
2ST-1IG	C1	2560	26	1.9	108
	C2	2817	26	2.0	108
	C3	2829	25	1.6	94
	C4	2868	25	1.5	99
	C5	2785	24	1.4	90
	C6	3037	25	1.3	91
CB-2ST-1IG	C1	2645	27	1.8	102
	C2	2785	24	1.7	95
	C3	2816	25	1.4	95
	C4	2996	24	1.5	98
	C5	2880	24	1.5	96
	C6	2908	24	1.3	92
2ST-1IG	C2	2667	27	2.1	103
	C3	2791	25	1.8	109
	C4	2670	27	1.9	101
$LSD_{0.05}$		252	2	0.4	8
SE		126	1	0.2	4

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A7. Mean agronomic traits of parent composites for each strategy of the late maturity class grown at Ames, IA in 1993.

Entry		Yield	Maturity	Lodging	Height
		----kg ha^{-1}----	----days[a]----	----score[b]----	----cm----
	C0	2440	34	2.8	97
2ST-1IG	C1	2425	34	2.8	91
	C2	2511	34	3.0	95
	C3	2410	34	2.8	87
	C4	2633	34	2.9	101
	C5	2557	34	2.9	91
	C6	2762	34	2.8	95
CB-2ST-1IG	C1	2504	34	3.1	101
	C2	2628	34	2.8	82
	C3	2815	35	2.8	91
	C4	3025	34	2.1	97
	C5	2923	34	2.6	97
	C6	2914	34	2.9	93
$LSD_{0.05}$		235	1	0.4	13
SE		118	1	0.2	7

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A8. Mean agronomic traits of parent composites for each strategy of the late maturity class grown at Stuart, IA in 1993.

Entry		Yield	Lodging	Height
		-----kg ha^{-1}-----	-----score[a]-----	-----cm-----
	C0	1967	1.9	85
2ST-1IG	C1	2130	1.9	83
	C2	2036	1.3	76
	C3	2186	1.4	81
	C4	2031	1.4	80
	C5	2152	1.2	77
	C6	2278	1.2	76
CB-2ST-1IG	C1	2074	1.5	78
	C2	2107	1.4	80
	C3	2026	1.4	75
	C4	2429	1.5	84
	C5	2399	1.6	78
	C6	2387	1.3	78
$LSD_{0.05}$		278	0.4	9
SE		139	0.2	5

[a]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A9. Mean agronomic traits of parent composites for each strategy of the late maturity class grown at Fairfield, IA in 1993.

Entry		Yield	Maturity	Lodging	Height
		----kg ha^{-1}----	----days[a]----	----score[b]----	----cm----
	C0	2781	31	1.4	95
2ST-1IG	C1	2707	29	2.0	89
	C2	2797	27	1.2	80
	C3	2918	28	1.3	85
	C4	2998	30	1.4	89
	C5	2793	30	1.4	83
	C6	2889	29	2.2	86
CB-2ST-1IG	C1	2732	27	1.3	84
	C2	3021	28	1.4	89
	C3	3000	29	1.6	94
	C4	3043	28	1.4	89
	C5	3056	30	1.4	80
	C6	2973	28	1.5	92
$LSD_{0.05}$		325	2	0.6	10
SE		162	1	0.3	5

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A10. Mean agronomic traits of parent composites for each strategy of the early maturity class grown at Ames, IA in 1994.

Entry		Yield	Maturity	Lodging	Height
		----kg ha^{-1}----	----days[a]----	----score[b]----	----cm----
	C0	3490	7	4.3	75
2ST-1IG	C1	3686	13	2.3	112
	C2	3873	14	2.5	110
	C3	3906	12	1.7	95
	C4	4160	10	2.1	94
	C5	4155	14	1.7	92
	C6	4459	13	1.8	93
CB-2ST-1IG	C1	3571	13	2.4	99
	C2	3883	14	1.7	102
	C3	3928	12	1.8	95
	C4	4063	13	1.8	90
	C5	4133	16	1.7	93
	C6	4197	13	1.6	95
$LSD_{0.05}$		246	2	0.2	21
SE		123	1	0.1	11

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A11. Mean agronomic traits of parent composites for each strategy of the early maturity class grown at Pocahontas, IA in 1994.

Entry		Yield	Lodging	Height
		-----kg ha^{-1}-----	-----score[a]-----	-----cm-----
	C0	2842	2.5	100
2ST-1IG	C1	2768	2.6	110
	C2	2686	2.2	96
	C3	2775	2.1	104
	C4	3174	2.1	93
	C5	3238	2.3	90
	C6	3028	2.1	89
CB-2ST-1IG	C1	2461	2.4	90
	C2	2663	2.6	97
	C3	2751	2.3	90
	C4	3022	1.9	87
	C5	2616	2.1	93
	C6	2688	1.9	89
$LSD_{0.05}$		520	0.5	13
SE		260	0.3	7

[a]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A12. Mean agronomic traits of parent composites for each strategy of the early maturity class grown at Kanawha, IA in 1994.

Entry		Yield	Maturity	Lodging	Height
		----kg ha^{-1}----	----days[a]----	----score[b]----	----cm----
	C0	3009	7	2.3	103
2ST-1IG	C1	3095	14	2.6	116
	C2	3211	16	2.1	110
	C3	3239	15	2.0	107
	C4	3592	12	1.9	102
	C5	3485	12	1.9	99
	C6	3540	15	2.0	110
CB-2ST-1IG	C1	3237	13	3.1	103
	C2	3262	16	2.4	104
	C3	3289	14	2.2	102
	C4	3353	11	1.9	99
	C5	3475	19	1.9	107
	C6	3277	14	1.7	95
$LSD_{0.05}$		299	2	0.5	10
SE		150	1	0.3	5

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A13. Mean agronomic traits of parent composites for each strategy of the midseason maturity class grown at Ames, IA in 1994.

Entry		Yield	Maturity	Lodging	Height
		-----kg ha^{-1}-----	-----days[a]-----	-----score[b]-----	-----cm-----
	C0	3573	18	2.6	103
2ST-1IG	C1	3574	19	2.3	118
	C2	3683	23	2.3	112
	C3	3926	18	2.3	106
	C4	3842	19	2.4	106
	C5	3836	18	2.3	108
	C6	3914	18	2.3	110
CB-2ST-1IG	C1	3793	22	2.6	106
	C2	3811	25	2.5	61
	C3	4114	26	2.3	94
	C4	4028	22	2.7	91
	C5	4361	23	2.4	96
	C6	4197	23	2.3	114
2ST-1IG	C2	3579	27	2.9	119
	C3	3789	21	2.7	131
	C4	3352	28	2.8	122
$LSD_{0.05}$		327	5	0.4	12
SE		164	3	0.2	6

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A14. Mean agronomic traits of parent composites for each strategy of the midseason maturity class grown at Keystone, IA in 1994.

Entry		Yield	Lodging	Height
		----kg ha^{-1}----	----score[a]----	----cm----
	C0	2456	2.5	102
2ST-1IG	C1	2311	3.0	113
	C2	2139	3.5	107
	C3	2481	1.9	100
	C4	2626	1.6	99
	C5	2592	2.6	101
	C6	2634	1.8	101
CB-2ST-1IG	C1	2301	3.0	109
	C2	2420	3.8	105
	C3	2394	3.6	97
	C4	2813	3.0	103
	C5	2054	3.0	94
	C6	2637	1.6	90
2ST-3IG	C2	2330	2.8	113
	C3	2547	2.2	117
	C4	2452	3.8	111
$LSD_{0.05}$		468	1	8
SE		234	1	4

[a]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A15. Mean agronomic traits of parent composites for each strategy of the midseason maturity class grown at Stuart, IA in 1994.

Entry		Yield	Maturity	Lodging	Height
		----kg ha^{-1}----	----days[a]----	----score[b]----	----cm----
	C0	3191	10	1.9	117
2ST-1IG	C1	3326	15	2.0	122
	C2	3241	14	2.3	121
	C3	3364	12	1.7	107
	C4	3196	12	1.6	110
	C5	3486	12	1.6	111
	C6	3393	12	2.3	107
CB-2ST-1IG	C1	3514	15	2.4	120
	C2	3245	13	1.8	114
	C3	3531	14	1.7	105
	C4	3687	13	1.9	107
	C5	3372	15	1.8	109
	C6	3528	15	1.8	108
2ST-1IG	C2	3087	14	2.4	126
	C3	2995	13	2.5	123
	C4	3229	14	2.3	120
$LSD_{0.05}$		395	2	0.6	10
SE		198	1	0.3	5

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A16. Mean agronomic traits of parent composites for each strategy of the late maturity class grown at Ames, IA in 1994.

Entry		Yield	Maturity	Lodging	Height
		-----kg ha^{-1}-----	-----days[a]-----	-----score[b]-----	-----cm-----
	C0	3656	33	2.3	124
2ST-1IG	C1	3496	32	3.1	119
	C2	3507	30	3.3	121
	C3	3663	33	3.4	126
	C4	3721	31	2.4	119
	C5	4014	35	2.0	114
	C6	4230	33	1.9	112
CB-2ST-1IG	C1	3595	31	2.8	119
	C2	4048	29	2.5	122
	C3	3775	32	3.2	117
	C4	4260	33	3.4	120
	C5	3874	32	3.3	114
	C6	4041	33	2.3	114
$LSD_{0.05}$		617	4	1.0	1
SE		308	2	0.5	1

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A17. Mean agronomic traits of parent composites for each strategy of the late maturity class grown at Fairfield, IA in 1994.

Entry		Yield	Lodging	Height
		-----kg ha^{-1}-----	-----score[a]-----	-----cm-----
	C0	3632	2.4	122
2ST-1IG	C1	3593	2.5	119
	C2	3760	2.3	118
	C3	3973	2.2	117
	C4	3848	2.2	121
	C5	3656	2.5	117
	C6	4122	2.1	105
CB-2ST-1IG	C1	3596	2.3	117
	C2	3750	2.2	108
	C3	3888	2.6	119
	C4	4017	2.4	104
	C5	4029	2.7	112
	C6	4137	2.1	113
$LSD_{0.05}$		247	0.5	20
SE		124	0.3	9

[a]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A18. Mean agronomic traits of parent composites for each strategy of the late maturity class grown at Stuart, IA in 1994.

Entry		Yield	Maturity	Lodging	Height
		----kg ha^{-1}----	----days[a]----	----score[b]----	----cm----
	C0	3026	25	2.1	129
2ST-1IG	C1	3330	24	2.7	127
	C2	3237	21	2.4	123
	C3	3415	24	2.5	122
	C4	3325	23	2.3	128
	C5	3232	22	2.4	115
	C6	3095	22	2.6	114
CB-2ST-1IG	C1	3182	22	3.0	113
	C2	3433	20	2.5	113
	C3	3348	24	2.6	125
	C4	3562	23	1.9	116
	C5	3421	23	2.2	114
	C6	3577	21	1.9	117
$LSD_{0.05}$		427	2	0.6	11
SE		214	1	0.3	5

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A19. Mean yield, maturity, lodging score, and height averaged across all environments for cycle 6 parental lines of the early maturity class.

Method	Entry	Yield	Maturity	Lodging	Height
		---kg ha^{-1}---	-----days[a]-----	-----score[b]-----	-----cm-----
2ST-1IG	A92-533002	3152	20	1.7	78
	A92-533004	3352	22	1.8	86
	A92-533013	3145	21	1.8	84
	A92-533014	3243	22	1.6	84
	A92-533019	3204	22	2.0	84
	A92-533020	3016	20	1.8	82
	A92-533023	3086	21	1.7	82
	A92-533024	3155	22	1.9	85
	A92-533025	3392	17	1.5	80
	A92-533026	3287	23	2.0	92

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A19. (continued)

Method	Entry	Yield	Maturity	Lodging	Height
		---kg ha^{-1}---	----days[a]----	----score[b]----	----cm----
CB-2ST-1IG	A92-534001	2837	21	1.5	72
	A92-534009	2992	21	1.7	82
	A92-534010	2907	19	1.9	75
	A92-534015	3029	23	1.7	84
	A92-534017	2998	22	1.6	77
	A92-534018	2875	18	1.4	69
	A92-534022	2921	23	1.7	78
	A92-534023	3157	16	1.7	78
	A92-534025	2874	18	1.3	70
	A92-533027	2924	20	1.6	78
$LSD_{0.05}$		136	1	0.2	5
SE		69	1	0.1	2

Table A20. Mean yield, maturity, lodging score, and height averaged across all environments for cycle 4 and cycle 6 parental lines of the midseason maturity class.

Cycle	Method	Entry	Yield	Maturity	Lodging	Height
			---kg ha^{-1}---	----days[a]----	----score[b]----	-----cm-----
C4	2ST-1IG	A86-207002	2915	21	2.1	97
		A86-207004	2806	19	1.9	84
		A86-207011	2919	19	1.7	89
		A86-207012	2726	21	2.1	99
		A86-207013	2855	22	2.0	93
		A86-207015	2817	22	1.4	88
		A86-207019	2868	19	1.9	88
		A86-207020	3040	19	1.3	80
		A86-207023	2684	21	1.7	96
		A86-207027	2798	18	1.9	95
C4	CB-2ST-1IG	A86-206004	3069	20	2.0	82
		A86-206005	2894	23	2.0	88
		A86-206011	2973	22	2.6	86
		A86-206014	2998	18	1.8	86
		A86-206016	2908	25	2.2	91
		A86-206019	2949	19	1.5	84
		A86-206021	2906	21	2.4	93
		A86-206022	3018	22	2.1	94
		A86-206024	3068	23	2.1	88
		A86-206026	2938	19	2.1	81

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A20. (continued)

Cycle	Method	Entry	Yield	Maturity	Lodging	Height
			---kg ha^{-1}---	---days[a]---	---score[b]---	---cm---
C4	2ST-3IG	A89-242001	3037	26	2.1	94
		A89-242002	2800	21	2.2	105
		A89-242004	2855	24	2.6	95
		A89-242006	2738	22	3.0	104
		A89-242007	2518	29	2.8	100
		A89-242013	2546	20	2.0	95
		A89-242014	2902	23	1.7	92
		A89-242016	2803	19	1.9	89
		A89-242022	2633	15	2.5	101
		A89-242025	2490	21	3.1	102
C6	2ST-1IG	A92-631004	2989	22	2.0	93
		A92-631007	2804	20	2.1	85
		A92-631008	3011	19	1.7	89
		A92-631010	3037	21	1.6	91
		A92-631013	3015	22	2.0	94
		A92-631014	2938	22	1.5	88
		A92-631018	2710	22	2.2	88
		A92-631019	2700	19	1.8	85
		A92-631024	2738	21	2.0	84
		A92-631026	2933	19	1.7	85

Table A20. (continued)

Cycle	Method	Entry	Yield	Maturity	Lodging	Height
			---kg ha^{-1}---	----days[a]----	----score[b]----	-----cm-----
C6	CB-2ST-1IG	A92-632005	2880	24	2.3	89
		A92-632009	3224	18	1.4	85
		A92-632010	3066	21	1.7	90
		A92-632012	3119	22	1.7	85
		A92-632013	3077	23	1.9	86
		A92-632014	2920	22	1.9	88
		A92-632018	3096	22	2.1	89
		A92-632024	3196	18	1.5	86
		A92-632027	2977	23	1.6	93
		A92-632030	3012	27	2.0	88
$LSD_{0.05}$			131	1	0.2	4
SE			67	1	0.1	2

Table A21. Mean yield, maturity, lodging score, and height averaged across all environments for cycle 6 parental lines of the late maturity class.

Method	Entry	Yield	Maturity	Lodging	Height
		---kg ha^{-1}---	-----days[a]-----	-----score[b]-----	-----cm-----
2ST-1IG	A92-731002	3068	29	1.9	97
	A92-731003	3092	26	1.8	85
	A92-731006	3005	30	2.4	100
	A92-731010	3033	30	2.5	102
	A92-731018	3108	30	2.2	96
	A92-731022	3115	31	1.9	102
	A92-731024	3120	29	2.1	100
	A92-731026	3077	29	1.8	94
	A92-731029	3025	28	1.8	97
	A92-731030	3129	27	1.9	96

[a]Days after August 31 when 95% of pods have reached the mature color.

[b]Scored on a scale of 1 (all plants erect) to 5 (all plants prostrate).

Table A21. (continued)

Method	Entry	Yield	Maturity	Lodging	Height
		----kg ha^{-1}----	-----days[a]-----	-----score[b]-----	-----cm-----
CB-2ST-1IG	A92-732002	3560	28	2.0	90
	A92-732004	3529	28	2.3	93
	A92-732007	3568	27	1.5	86
	A92-732009	3488	28	2.5	99
	A92-732013	3351	29	2.5	105
	A92-732017	3498	27	2.5	99
	A92-732023	3236	28	1.4	88
	A92-732027	3016	31	1.8	97
	A92-732029	3152	29	1.8	102
	A92-732030	3127	28	2.1	100
$LSD_{0.05}$		140	1	0.2	4
SE		71	1	0.1	2

REFERENCES

Altman, D.W., and R.H. Busch. 1984. Random intermating before selection in spring wheat. Crop Sci. 24:1085-1089.

Avey, D. P., H.W. Ohm, F.L. Patterson, and W.E. Nyquist. 1982. Three cycles of simple recurrent selection for early heading in winter wheat. Crop Sci. 22:908-911.

Bos, I. 1977. More arguments against intermating F_2 plants of a self-fertilizing crop. Euphytica 26:33-46.

Brim, C.A., and J.W. Burton. 1979. Recurrent selection in soybeans II. Selection for increased percent protein in seeds. Crop Sci. 19:494-498.

Carver, B.F., J.W. Burton, R.F. Wilson, and T.E. Carter. 1986. Cumulative response to various recurrent selection schemes in soybean: Oil quality and correlated agronomic traits. Crop Sci. 26:853-858.

Comstock, R.E. 1977. Quantitative genetics and the design of breeding programs. p. 705-718. In E. Pollak, O. Kempthorne, and T. B. Bailey, Jr. (ed.) Proceedings of the International Conference on Quantitative Genetics. The Iowa State University Press, Ames, IA.

Fehr, W.R. 1987. Principles of cultivar development. Volume I. Theory and Technique. Macmillan Publishing Company, Macmillan, Inc. New York.

Fehr, W.R., and L.B. Ortiz. 1975. Registration of a soybean germplasm population. Crop Sci. 15:739.

Guimaraes, E.P, and W.R. Fehr. 1989. Alternative strategies of recurrent selection for seed yield of soybean. Euphytica. 40:111-120.

Hallauer, A.R. 1981. Selection and breeding methods. p. 3-55. In K. J. Frey (ed.) Plant Breeding II. Iowa State Press, Ames, IA.

Hanson, W.D. 1959. The breakup of initial linkage blocks under selected mating systems. Genetics 44:857-868.

Hanson, W.D. 1992. Phenotypic recurrent selection for modified reproductive period in soybean. Crop Sci. 32:968-972.

Hull, F.H. 1945. Recurrent selection for specific combining ability in corn. J. Amer. Soc. Agron. 37:134-145.

Hull, F.H. 1952. Recurrent selection and overdominance. p. 451-473. In J. W. Gowen (ed.) Heterosis. The Iowa State University Press, Ames, IA.

Jenkins, M.T. 1940. The segregation of genes affecting yield of grain in maize. J. Amer. Soc. Agron. 32:55-63.

Kenworthy, W.J., and C.A. Brim. 1979. Recurrent selection in soybeans: I. Seed yield. Crop Sci. 19:315-318.

Klein, S.J., M.A. Smith, and K.J. Frey. 1993. Recurrent selection for test weight and grain yield of oat. Crop Sci. 33:744-749.

Meredith, W.R., Jr., and R.R. Bridge. 1973. Recurrent selection for lint percent within a cultivar of cotton (Gossypium hirsutum L.). Crop Sci. 11:695-698.

Miller, J.E., and W.R. Fehr. 1979. Direct and indirect recurrent selection for protein in soybeans. Crop Sci. 19:101-106.

Miller, P.A., and J.O. Rawlings. 1967. Breakup of initial linkage blocks through intermating in a cotton breeding population. Crop Sci. 7:199-204.

Pederson, D.G. 1974. Arguments against intermating before selection in a self-fertilising species. Theor. Appl. Gen. 45:157-162.

Piper, T.E., and W.R. Fehr. 1987. Yield improvement in a soybean population by utilizing alternative strategies of recurrent selection. Crop Sci. 27:172-178.

Prohaska, K.R., and W.R. Fehr. 1981. Recurrent selection for resistance to iron deficiency chlorosis in soybeans. Crop Sci. 21:524-526.

SAS Institute. 1992. SAS guide for personal computers. 6th ed. SAS Inst., Inc., Cary, NC.

Steel, R.G.D., and J.H. Torrie. 1980. Principles and procedures of statistics. A biometrical approach. McGraw-Hill, Inc.

Stuthman, D.D., and R.E. Stucker. 1976. Recurrent selection for yield in oats. Agron. Abstr. American Society of Agronomy, Madison, WI. p. 63.

Sumarno, and W.R. Fehr. 1982. Response to recurrent selection for yield in soybeans. Crop Sci. 22:295-299.

Tinius, C.N., J.W. Burton, and T.E. Carter. 1992. Recurrent selection for seed size in

soybean: II. Indirect effects on seed growth rate. Crop Sci. 32:1480-1483.

Walker, A.K., and A.F. Schmitthenner. 1984. Recurrent selection for tolerance to phytophthora rot in soybean. Crop Sci. 21:495-497.

Yunus, M., and R.S. Paroda. 1982. Impact of biparental mating on correlation coefficients in bread wheat. Theor. Appl. Genet. 62:337-343.

ACKNOWLEDGMENTS

I, first and foremost, wish to thank Dr. Walter R. Fehr for his patient efforts in guiding my studies while at Iowa State. I would also like to thank Drs. Paul Hinz, Kendall Lamkey, Randy Shoemaker, David Webb, and Richard Willham for serving as members of my graduate committee.

I would also like to express my thanks to Grace Welke, Steve Shultz, and Dan Weber for the help and good advice they have given me over the years.

Thanks is also extended to former graduate student Richard Hartmann whose intellectual acumen and sense of humor made life a little easier.

Finally, I would like to thank my long suffering parents for their patience and support. After seeing two sons enroll in graduate school, I'm sure they think the term 'Ph.D' stands for 'phinally done.'